## Book Review

ANDERSON, D. T. 1973. Embryology and Phylogeny in Annelids and Arthropods. International Series of Monographs in Pure and Applied Biology. Vol. 50. Pergamon Press, Oxford and New York. xiv + 495 pp., 164 text-figures, 4 tables, author, subject and generic name indices. Cloth - $24.00 (U.S.).

Does the phylum Arthropoda constitute a monophyletic or a polyphyletic taxon? This question has been a source of controversy among zoological systematists for many years because of a lack of fossil forms bridging important gaps between the major arthropod taxa and their possible precursors, and because evidence from "comparative anatomy and embryology has more commonly provided fuel for argument than for the resolution of problems". (Barnes, 1968).

Anderson's book is an important new contribution to this discussion, because of the plethora of previously unused embryological facts that he brings to bear on the subject. Since the author has published extensively on the embryology of polychaetes, oligochaetes, leeches, Onychophora, Crustacea, ticks, and flies, he is as qualified as anyone to write it.

The book consists of an Introduction (chapter 1) and nine chapters describing in detail the embryogenesis of polychaetes (2), oligochaetes and leeches (3), Onychophora (4), Myriapoda (5), apterygote (6) and pterygote (7), insects, Crustacea (8) and Chelicerata (9). Chapter 10 entitled "*A New Synthesis?*", summarizes the main conclusions of these chapters, his final conclusion being that "arthropodization has occurred at least twice, probably three times, and possibly more than three times" (p. 471). He thus supports Manton's (1973) thesis of a polyphyletic origin for the arthropods.

Each descriptive chapter has a similar organization: cleavage, presumptive areas of the blastula or blastoderm (i.e. fate maps), gastrulation, further development of the gut, development of external form, further development of the mesoderm and ectoderm, development of the head, and a concluding section: "*The Basic Pattern of Development*" in which previous sections are summarized and phylogenetic implications derived. Each concluding section is organized in such a way that one can get the essence of the book by reading this part in each chapter, studying the illustrations, and reading chapter 10. The variation in embryogenesis occurring within each taxon is fully covered and cross references are made at pertinent points to similarities and differences existing in the development of a particular system in other arthropod taxa.

Coverage of the pterygote insects is less complete because of his two recent reviews (Anderson, 1972a, b) in Counce and Waddington's *Developmental Systems: Insects.* Anderson organizes his chapter on Chelicerata slightly differently too, leaving his discussion on fate maps until near the end. He does this because of a lack of detailed embryological information on some groups (nothing is known of embryogenesis in Palpigrada or Ricinulei) and because so much variability exists. An additional service he provides in this chapter, is to unify the terminology used in descriptions of chelicerate development, with that used in other groups.

The illustrations are another strong point in the book. They are fully labelled, clearly executed, and fully acknowledged line drawings. Unfortunately, he does not make as much use of these as he could have. Most figures contain five or six drawings and Anderson does not recognize this fact when he is referring to them in the text. For example, he might refer to Fig. 86, when, in fact, he should refer to Fig. 86j. A reader must thus spend a lot of time looking at the drawings in a particular figure, trying to decide which one Anderson is referring to in the text. In addition, no scale lines are included on the figures. These would be useful, for example, to one interested in comparing the size of yolk-rich and yolk-poor eggs of species within one taxon.

Although "*Phylogeny*" is part of the title of the book, there is not a single phylogenetic dendrogram included in it. I have long felt that the failure of an author to include these implies a lack of commitment to his phylogenetic conclusions. Using his discussions, I have illustrated his proposed phylogenies below (Fig. 1). As shown, Anderson recognizes three arthropod phyla: the Uniramia, Chelicerata, and Crustacea. He does not discuss phylogeny fully within his phylum Crustacea because of the absence of critical studies in many groups.

According to Anderson, neither the Crustacea nor the Chelicerata can be linked phylogenetically with the Uniramia and Annelida based on their embryogenies. Crustacean embryogenesis is based on a type of spiral cleavage different from that of annelids and, in addition, the presumptive areas in their blastulae or blastoderms are for a nauplius larva. Chelicerates have basically a specialized total cleavage and fate maps differing fundamentally from those of other arthropods. As can be seen from Figure 1, embryogenesis also supports the view that Onychophora, Myriapoda and Hexapoda form a unit, all originating from a common, lobopod ancestor. Protura are not included by Anderson in his discussion of Hexapoda because their embryogenesis is unknown.

Anyone familiar with the recent work of Dr. Sidnie M. Manton, will recognize the phylogenies summarized in Figure 1. They resemble hers except that she omits "speculative dichotomies"within subordinate taxa of the myriapods and hexapods (Manton, 1973). Also, her conclusions are based mostly on the structure and function of the adults of 'selected types' of Arthropoda.

Ghiselin (1974), in his review of Anderson's book, has remarked that his approach is typological also, "depending on abstractions of developmental archetypes - as Manton's depends upon functional morphological ones". According to Anderson, a basic pattern for each taxon is apparent in modified form among subordinate taxa. "But", say Ghiselin, "if organisms differ, they must have evolved, and why cannot developmental patterns evolve too?" As Ghiselin emphasizes "To demonstrate polyphyly, one has to relate two derived taxa from two divergent ancestral precursors". Neither Anderson nor Manton do this. Also, both workers sometimes forget that all living taxa are specialized to some extent. Thus one does not expect to find among the extant fauna, survivors of ancestral groups unmodified in form or development as related to the ancestral condition. "We are told that arthropods are not descended from annelids, when what is meant is that they are not derived from any known extant class of annelids." (Ghiselin, 1974).

Anderson places much emphasis on his carefully derived fate maps of the presumptive areas of the blastula or its equivalent. He does this because the blastula has the most stability of functional configuration of any stage that precedes or follows it, and because "the configuration can be epitomized in a fate map which effectively summarizes all that is important about the embryonic development of the animal in question from a comparative point of view" (p. 2).

Fate maps have been developed for echinoderms and for amphibians and other vertebrates using experimental techniques (Balinsky, 1970). Usually, such maps are derived by marking small groups of cells or single cells in the blastula or its equivalent stage of development with vital stains or "marker" mutations or in other ways and following these marked cells or their progeny to the places they occupy in the fully formed embryo (in some animals such artificial marking is not required because of the presence of pigmented, or yolk-containing, naturally-marked cells). With few exceptions, this has not been done with the animals treated in this book. Anderson's method (and the only one available in most cases) is to "extrapolate from subsequent events back on to the blastoderm areas in which parts are initiated" (Anderson, 1962). This is a painstaking task, which seems to work. However, we will not know how well until such marking studies have been made. Anderson's phylogeny depends almost completely on the accuracy of these maps.

When reading the phylogenetic sections of this book, one gets the distinct impression that

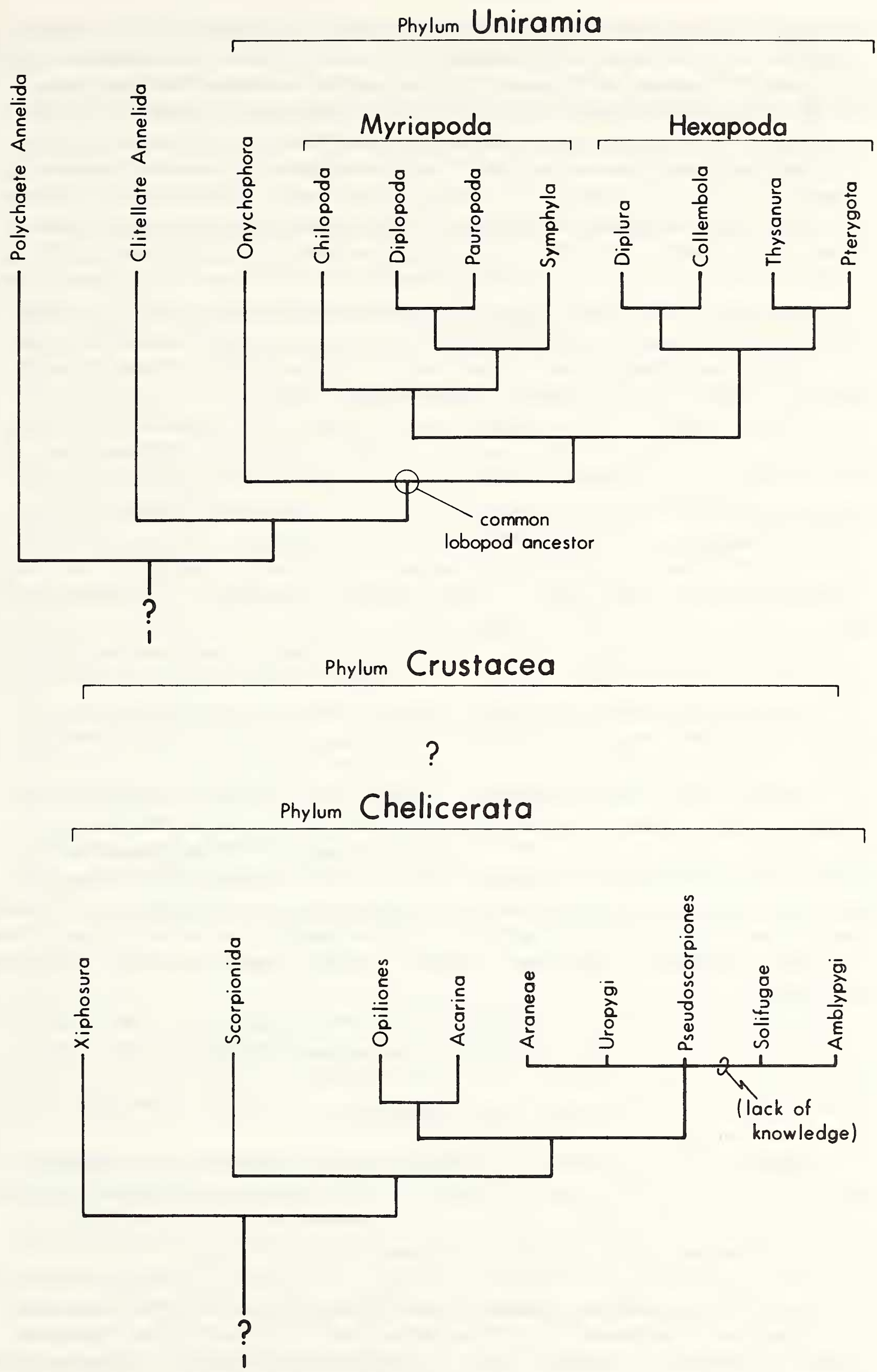


Fig. 1. The phylogeny of the three arthropod phyla based on Anderson's interpretation of comparative embryogenesis.

Anderson had already accepted Manton's ideas on arthropod phylogeny before he began writing (the book is dedicated to Dr. Manton). An indication of this is his treatment of head development in Crustacea and Chelicerata. He does not use the comparative information available on head development because "the earlier emphasis on the comparative segmental composition of the arthropod head in assessment of the phylogenetic relationships between major arthropod groups can now be seen to have been misplaced. It is becoming increasingly evident that the cephalization of the anterior end has occurred independently in each of the major groups of extant arthropods from simple beginnings which are unknown and probably unknowable for each" (p. 42). Thus, Anderson ignores evidence supporting a monophyletic origin for the arthropods. Siewing's (1969) recent book on animal development covers much of the same ground as Anderson's (but includes other invertebrates as well as the vertebrates) but with a very different approach. On page 381, Siewing has a section entitled "*Das Kopfproblem*", which thoroughly treats comparative head development. His conclusions are presented in a table on page 392. Anderson does not cite this work.

In addition, Anderson omits accounts of the embryogenesis of Tardigrada, Pentastomida, Pycnogonida, Echiuroidea, and Myzostomida in his book. As Ghiselin (1974) points out, these omissions are not explained. It is not because of the lack of embryological works on representative species of these taxa, because such works do exist (see Pflugfelder (1970): p. 174 - Tardigrada, p. 176 - Pentastomida, p. 209 - Pycnogonida, p. 121 - Echiuroidea. Incidentally, Pflugfelder's important book is omitted from Anderson's bibliography too). The phylogenetic position of the tardigrades, pentastomids and pycnogonids is problematical (eg. Barnes, 1968), but one would have thought this a good reason to include them in this book.

In another review of this book, Matsuda (1974) pinpoints what, I believe, is an additional flaw in Anderson's phylogenetic thinking: ". . .the validity of phylogenetic inference based on functional morphology, which Anderson accepts, should be at least discussed since the concept of phylogeny has always been based on homology of structure (and vice versa); discussion of this basic procedure in the study of phylogeny is dismissed in this work". The reason for this again, I think, is that Manton's ideas have held sway over Anderson's phylogenetic thinking ever since he did his thesis on polychaete embryology under her direction at the University of London (Anderson 1959). In her recent review (1973), Manton states that "Evidence from functional morphology and of new functional studies of embryology using fate maps (*Anderson's book*) indicates that Arthropods are probably polyphyletic. . ." Therefore, what transpires is that Anderson's conclusions, coloured by Manton's phylogenetic ideas, are used in turn by her to reinforce her own ideas on arthropod phylogeny based on functional morphology.

Gavin DeBeer's (1962) book "*Embryos and Ancestors*", treats homology, phylogeny and embryology in all of its complex ramifications, many of which are crucial in the context of Anderson's phylogenetic arguments. As Matsuda (1974) points out, this book is not mentioned by Anderson either. Is this because it was overlooked too, or because it presents ideas difficult for Anderson to include or rebut in his arguments?

In summary, I do not believe that the evidence Anderson marshalls is sufficient to support his conclusion that the arthropods are polyphyletic. His evidence can be used just as effectively in support of the alternate point of view, i.e. that arthropods are monophyletic (I have no quarrel with his conclusions on relationships among the subordinate taxa of the Myriapoda, Hexapoda or Chelicerata). As Ghiselin (1974) asked, ". . .why cannot developmental patterns evolve too?" DeBeer (1962) has pointed out that "New characters may appear at all stages of ontogeny and, by heterochrony, they may be retarded or accelerated so as to appear later or earlier in subsequent ontogenies". Also, ". . .variations of evolutionary significance can and do arise at the earliest stages of development". This probably occurred during the Pre-cambrian in the ontogeny of the lines arising from a common arthropod ancestor and giving rise to the extant classes of Arthropoda. Confronted with differing external conditions, these lines diverged, giving rise to the three different and distinct patterns of arthropod embryogenesis existing today. That this kind of divergent evolution is still occurring within each extant, major, arthropod taxon is evidenced by the heterochrony of development existing in each as summarized by Anderson, an excellent example being that of some brachyuran Crustacea in which the development of sequences of larval characteristics is accelerated such that they all occur within the egg. Extrapolating far into the future, it is not difficult to imagine differences in embryogenesis as great as those now separating Uniramia, Crustacea and Chelicerata arising in the Crustacea.

What was the developmental pattern of this arthropod ancestor like? Anderson provides one answer himself: "Spiral cleavage is wide spread among many phyla. . .". I see no difficulty in visualizing the three embryological patterns of the arthropods arising from this pattern through specialization and heterochrony. The early appearance of a trochophore larva in the annelid line and of a nauplius larva in the crustacean line were two ways of solving the problems confronting hatchlings in an aquatic environment.

The same reasoning can be used to explain the phylogenetic relationship between the Onychophora on the one hand, and the myriapods and hexapods on the other. As Anderson emphasizes, most Onychophora are viviparous, have secondarily yolkless eggs and a specialized mode of development. Oviparous species are rare, have a prolonged development and are practically unknown embryologically (p. 93). Therefore, the developmental evidence linking the Onychophora with the myriapods and hexapods is based primarily on events occurring in highly specialized species. Similarities in development of onychophorans and other Uniramia have probably arisen through convergence.

The remarks above can also be directed against Manton's phylogenetic conclusions. Both Anderson and Manton have worked exclusively with "selected types" of higher taxa. Undoubtedly, this approach has influenced their view of the events occurring at the population and species level - the level at which splitting of lines originally begins as a result of reproductive isolation and interactions between genotypes and environmental factors. Neither author seems to realize that big gaps can have little beginnings.

Questions of phylogeny aside, there is no up-to-date book in English on arthropod and annelid embryogenesis to compare with Anderson's. It is an attempt, and a very successful one, to bring order out of the chaos of the voluminous literature. No invertebrate embryologist or systematist, reductionist or otherwise, can afford to be without this book. It contains a prodigious amount of clearly described and well organized developmental information that has never been gathered together as effectively. In addition, Anderson's book is a guide to the many critical investigations that have yet to be made.

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